

CHAPTER 1

Microbial and Faunal Interactions as They Affect Soil Organic Matter Dynamics in Subtropical Agroecosystems

D. C. Coleman, P. F. Hendrix, M. H. Beare, W. X. Cheng,
and D. A. Crossley, Jr.

I. INTRODUCTION

In the last few years, there has been a significant increase in interest shown in sustainable agriculture, which has also been termed "alternative agriculture" (Pesek et al., 1989). Thus, several studies have been conducted in various parts of the world to assess the feasibilities of more closely linking inputs and outputs in agricultural systems, particularly in a holistic or landscape context (Elliott and Cole, 1989; Sanchez et al., 1989; Hendrix et al., 1990).

Our research at the University of Georgia has centered on the biological interactions which occur in agroecosystems, particularly those which are involved in the detrital food web (Hendrix et al., 1986; Coleman and Hendrix, 1988; Hendrix et al., 1990). Studies in Colorado (Holland and Coleman, 1987; Hunt et al., 1987) have used similar approaches. The strong effects of placing crop residues on the surface of the ground through no tillage (NT) apparently favor the growth and development of fungi, in contrast to the conventional tillage (CT) regime (deep moldboard plowing to ca. 15–20 cm depth), which may be bac-

terially dominated (Figure 1A, B). However, certain groups of bacteria, such as the denitrifiers, may be more active in the surface few centimeters of NT systems than in CT systems (Doran, 1980). A range of physical factors, such as available moisture and aeration, are important modifiers of microbial and faunal activities in these agroecosystems.

This chapter reviews progress which has been made in the last few years in agroecosystem studies in subtropical regions of the Georgia Piedmont, and delineates some of the areas of investigation which we are pursuing in our current studies.

II. MICROBIAL AND MICROBIAL/FAUNAL ACTIVITIES AND INTERACTIONS

In a series of field experiments in 1986–1987 captan (a N-trichloromethylthio-4-cyclohexane-1,2-dicarboximide fungicide with a relatively wide spectrum for inhibition of saprophytic fungi) was applied to rye residues (17.5 g/m², 47% active ingredients [a.i.]) in litter bags under field conditions. Fungal activity decreased by ca. 40–45% and total decomposition was correspondingly decreased (Figure 2A and B).

We have observed strong effects of litter (residue) placement on primary decomposition rates also, with significantly slower rates occurring in surface residues, compared to the buried residues in conventional tillage plots (Figure 2B). Other measures of ecosystem activity were markedly shifted, as a function of captan application. Thus total N (expressed as %N remaining) was lower in the captan treatment (Figure 2C), reflecting less immobilization in the absence of fungi (Figure 2B, NT), and C:N ratios of the litter were kept at or near 60 between late September and late April of the ca. 300-day experiment (Figure 2D, NT). As expected, there was no significant effect of captan treatment when the litter bags were buried, mimicking the burial due to plowing in CT. In addition, we measured fungal/bacterial ratios, using the substrate-induced respiration (SIR) method of Beare et al. (1990). There was a significantly higher proportion of fungi in the early stages of plant residue (rye = *Secale cereale*, and grain sorghum = *Sorghum bicolor*) decay, over the first 24 days of decomposition, gradually narrowing to 100 days (Table 1). By using suitable inhibitors of fungal and bacterial activity (cycloheximide and streptomycin sulfate, respectively), Neely et al. (in press) were able to reliably measure bacterial or fungal biomass as a function of the suitable SIR measurement (Table 1).

Mueller et al. (1990), and Crossley et al. (this chapter) followed changes in microarthropods (principally oribatid, mesostigmatid, and prostigmatid mites) in control and captan-treated litter bags following the inhibition of litter fungi in both CT and NT treatments. Mueller et al. (1990) noted significant shifts in litter decay rates after 4–6 months of steady exposure of the litter substrates to the fungicide. Several dominant fungivorous oribatid families (Oribatulidae, Oppiidae, and Haplozetidae) and one prostigmatid family (Tarsonemidae) were reduced in buried NT litter, and a similar pattern existed in buried CT litter

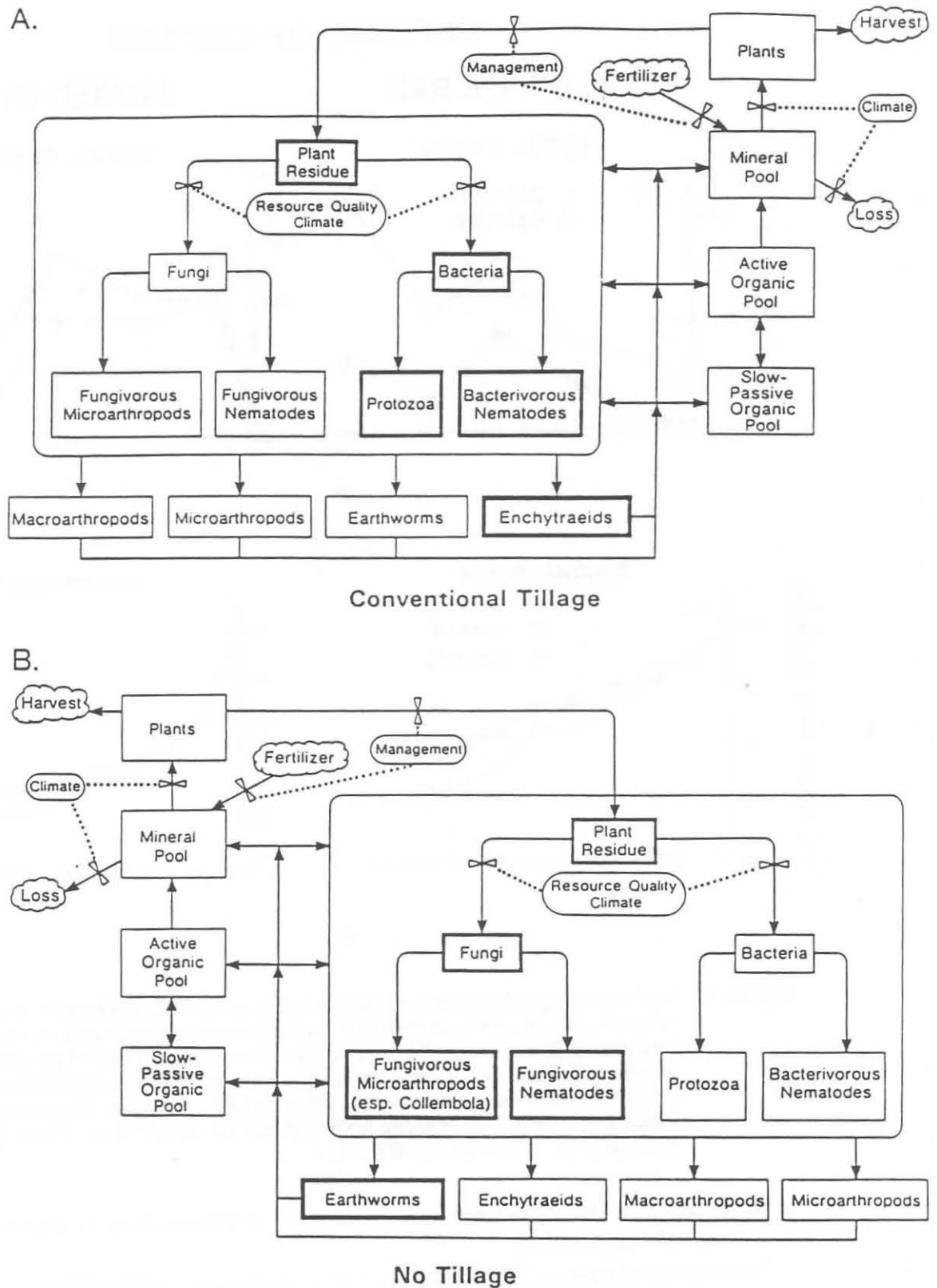


Figure 1. Conceptual models of detritus food webs in conventional tillage (A) and no tillage (B) agroecosystems. Boxes = nutrient storages, clouds = nutrient sources or sinks, and arrows = nutrient transfer pathways. Valve symbols on arrows indicate that nutrient transfers are influenced by factors connected with dotted lines. (From Hendrix, P. F. et al. 1986. *Bioscience* 36:374–380.)

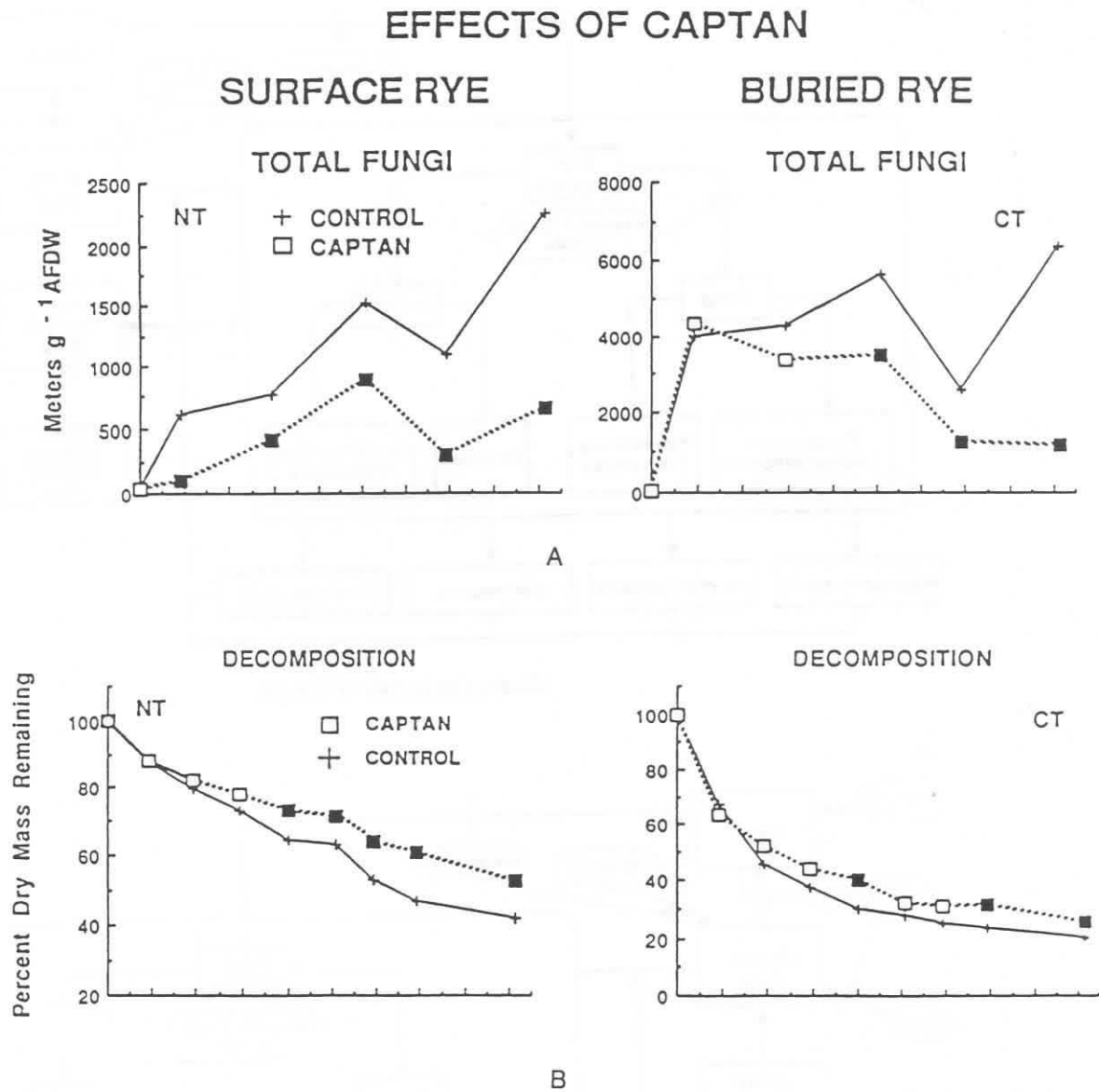


Figure 2. (A) Total fungi; (B) mean percent dry mass remaining; (C) total N; and (D) C:N ratios in surface and buried rye litter bags from control treatments (+) and captan treatments (□) in NT and CT agroecosystems. Effects of individual biocide treatments on measured parameters are shown only where a significant difference ($p < 0.05$) from controls was detected in at least one tillage. Blackened symbols indicate significant differences from controls by sample date. (From Beare, M. H. et al., *Ecol. Monogr.* 62:569–591.)

relative to controls. Thus there was a trophic level reaction to deprivation or curtailing of fungal food.

More general system-level responses were measured by Hendrix et al. (1987) and Beare et al. (1992), who measured total soil respiration in both CT and NT plots. There was significantly more CO_2 output in the NT plots during the drought year of 1986–1987. In addition, Hendrix et al. (1987) assigned production and respiration values to heterotrophic fauna and microbes, measuring a surprisingly

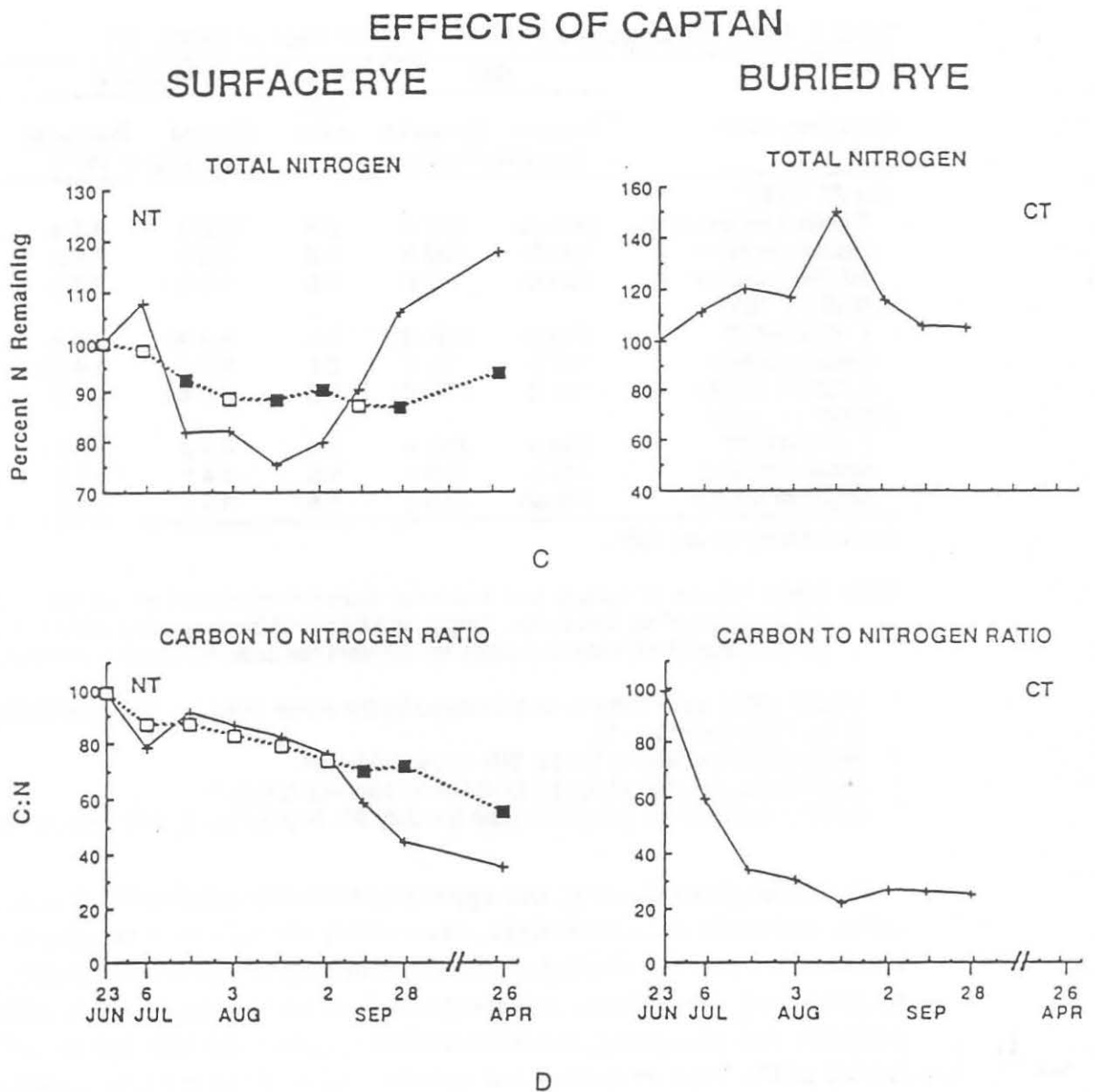


Figure 2 (continued).

high proportion (ca. 30%, due to earthworms) integrated over an entire ca. 170-day cool growing season (Table 2).

Other studies, summarized by Parmelee et al. (1990), examined the impacts of the biocide, carbofuran, on reducing earthworm numbers and activities in NT and CT experimental enclosures. Carbofuran plots had reduced earthworm and enchytraeid biomass (to less than 10% of control enclosures) and as much as 47% greater coarse particulate organic matter than the control plots (Table 3). This difference was largely attributable to earthworm activities, but there were also detectable non-target effects of the carbofuran on some of the decomposer microflora (bacteria), as measured in independent litter bag decomposition trials. These non-target effects were estimated to be about 12% of the total difference in litter bag decomposition effects, in biocide vs non-biocide control plots.

Table 1. Litter Decomposition Studies in Litter Bags at Griffin, GA

Sampling date ^a	SIR		F:B ^b SIR ratio	Biomass		F:B ^c Biomass ratio
	Fungal ($\mu\text{g CO}_2\text{-C/g/hr}$)	Bacterial		Fungal ($\mu\text{g C/g} \times 10^{-3}$)	Bacterial	
July 27, 1987						
<i>Trifolium incarnatum</i>	547 ab	237 a	2.5	10.6 a	4.3 a	2.5
<i>Secale cereale</i> ^d	448 b	283 a	1.6	7.6 b	3.6 a	2.1
<i>Sorghum bicolor</i>	224 c	91 b	2.5	4.7 c	1.9 b	2.5
August 24, 1987						
<i>T. incarnatum</i>	313 a	176 ab	2.5	5.4 ab	3.3 a	1.6
<i>Secale cereale</i> ^d	188 b	91 b	2.0	2.9 c	1.4 bc	2.1
<i>Sorghum bicolor</i>	198 b	177 ab	1.3	3.7 bc	1.7 b	2.2
October 11, 1987						
<i>T. incarnatum</i>	234 a	260 a	0.9	4.3 a	3.9 a	1.1
<i>Secale cereale</i> ^d	165 b	113 c	1.5	1.4 b	1.5 c	0.9
<i>Sorghum bicolor</i>	178 ab	110 c	1.6	3.3 a	1.6 c	2.1

Source: Neely et al., 1991.

Note: Mean values of fungal and bacterial substrate-induced respiration (SIR), fungal:bacterial (F:B) SIR ratios, fungal and bacterial biomass measurements, and fungal:bacterial (F:B) biomass ratios for all plant residues for three sample dates.

^a Values within each sample date followed by the same letter are not significantly different at the 0.05 level ($p > F$).

^b Represents the ratio of fungal SIR to bacterial SIR.

^c Represents the ratio of fungal biomass to bacterial biomass.

^d Days in the field for *Secale cereale* are July 20, September 3, and October 18, 1987.

In a more general sense, our agroecosystems are interlinked in several interesting and quite redundant ways, ones which are only now becoming apparent to research scientists. Having concentrated in the past on more short-term changes in gross crop litter decay and inorganic ions of interest (such as nitrate, ammonium, and phosphate) we have tended to ignore the changes in soil organic matter status, both in quality and quantity. Also, there are new concerns about the larger milieu in which this action is occurring. Thus we have the actors and the play, but the theater (i.e., the physical substrate and landscape) must be considered as an integral factor. We now turn our attention to that facet of our current, ongoing research.

III. CURRENT GEORGIA AGROECOSYSTEM STUDIES

Our objectives include an investigation of the regulatory roles of plant roots, saprophytic fungi, micro-arthropods, and earthworms on turnover and stabilization of carbon and nitrogen in water-stable aggregates. We are studying these processes by following transformations of C and N from plant litter to soil pools and plant biomass in fields with two contrasting management approaches: (1) no tillage grain sorghum/winter wheat (soil organic matter [SOM] aggrading, i.e., increasing in organic matter [OM] content), and (2) intensive tillage grain sorghum/fallow (SOM degrading) agroecosystems, which are described below.

Table 2. Estimated C Standing Stocks, Biotic Production, and Respiratory Loss by Major Biotic Groups in CT and NT Agroecosystems

Biotic group	Average standing stock (g C/m ²)		Production ^a (g C/m ²)		Respiration ^a (g C/m ²)	
	CT	NT	CT	NT	CT	NT
Bacteria	69	44	143 (138–148)	92 (88–95)	213	137
Fungi	15	16	10 (9–11)	11 (10–12)	15	16
Protozoans	5	4	10 (3–50)	8 (2–40)	20	16
Nematodes	0.2	0.1	0.6 (0.4–0.8)	0.3 (0.2–0.4)	1	0.5
Microarthropods	0.07	0.2	0.1 (0.04–0.2)	0.3 (0.1–0.5)	0.2	0.6
Macroarthropods	0.004	0.02	0.004 (0.001–0.006)	0.02 (0.006–0.03)	0.02	0.07
Enchytraeids	0.03	0.01	0.05 (0.02–0.08)	0.02 (0.005–0.03)	0.1	0.05
Earthworms	2	10	4 (0.4–6)	20 (2–30)	14	71
Total	91	74	168	132	263	241

Source: Hendrix et al., 1987.

Note: Values are for cool season (winter/spring) grain rye crops and soil superficial (0–15 cm) layer.

^a Production (P) values are given as a mean (or conservative estimate for protozoans and earthworms) followed by range (in parentheses), based on the range of P/B values in the literature. Respiration (R) was calculated from mean production using an average of literature P/R estimates. See text for references.

Our approaches include a quantification of the effects of each biotic manipulation on: (1) particulate OM decomposition and biotic abundances; (2) aggregate formation and stabilization; and (3) aggregate associated and bulk soil pools of particulate, active-unprotected, active-protected, passive, and soil solution organic C and N.

A. Experimental Methods and Sites

We have three main research sites ranging from sandy loam to sandy clay loam Kanhapludult soils in the Georgia Piedmont (Figure 3): (1) the Horseshoe Bend (HSB) site, in a floodplain near Athens, GA; (2) Dawson field, an upland site with moderate to extensive erosion, at Watkinsville, GA; and (3) a field site at Griffin, GA (GRF) (Figure 3). Sites 1 and 3 are being managed to degrade the organic matter status from an existing fescue (*Festuca* sp.) grassland (GRF) and mixed grass at HSB (descending curve, Figure 4), while Site 2 is being managed to an aggrading treatment to increase organic matter content and quality similar to that shown in the ascending curve of Figure 4. We suggest that organic matter quality, including microbial biomass in our aluminum sesquioxide well-

Table 3. Standing stock of Fine Coarse, and Total Organic Matter (Fine + Coarse) to a Depth of 15 cm in No Tillage and Conventional Tillage Control and Carbofuran-Treated Pens 139 (November 10, 1986) and 292 (April 12, 1987) Days after Initial Application

		Organic matter		Differences (% of control)
		Control	Carbofuran	
November 10, 1986				
NT				
Fine ^a	193.85 ± 12.01	281.76 ± 28.82 ^c	45	
Coarse ^b	485.46 ± 43.33	639.39 ± 35.57	32	
Total	687.74 ± 52.75	921.30 ± 47.15 ^c	34	
CT				
Fine ^a	248.57 ± 22.71	291.27 ± 19.13	17	
Coarse ^b	527.61 ± 118.67	478.03 ± 73.44	-9	
Total	776.26 ± 126.32	779.83 ± 88.38	1	
April 12, 1987				
NT				
Fine ^a	119.11 ± 6.18	170.07 ± 16.27 ^c	43	
Coarse ^b	595.55 ± 71.90	775.91 ± 134.01	30	
Total	714.66 ± 75.16	945.98 ± 133.14	32	
CT				
Fine ^a	157.22 ± 8.38	170.24 ± 12.0	8	
Coarse ^b	266.88 ± 34.33	470.88 ± 46.48 ^c	76	
Total	424.10 ± 39.55	641.12 ± 52.22 ^c	51	

Source: Parmelee et al., 1990.

Note: Standing stock, g ash-free dry weight/m²; initial application, $n = 12 \bar{x} \pm 1$ SE; NT = no tillage; CT = conventional tillage.

^a >0.79 mm, <2.38 mm.

^b >2.38 mm.

^c Significantly different from control at $p = 0.05$.

weathered Ultisols may be an important characteristic influencing the rate of degradation or aggradation of organic matter in southeastern Piedmont soils.

Next are discussed some early research results, and syntheses from the first year of field work in the three study sites.

B. Earthworm Effects on Soil Morphology

West et al. (1991) conducted laboratory and field experiments (with and without earthworms) on soils from Watkinsville, GA, which had been under slight, medium, or heavy erosion histories. Loamy sand and sandy clay loam soils were collected, thin sectioned, and examined microscopically for fabric and porosity characteristics.

In both soil types, fewer and smaller voids were present adjacent to earthworm channels. In the sandy soil, coatings comprised of a combination of clay, organic matter, and clay-organic complexes were observed along the channel walls. West et al. (1991) inferred that the clay-organic materials were deposited in the channel walls, whereas the coarser sandy materials were deposited within the earthworm channels or in surface castings. In no tillage or direct-drilled agroecosystems,

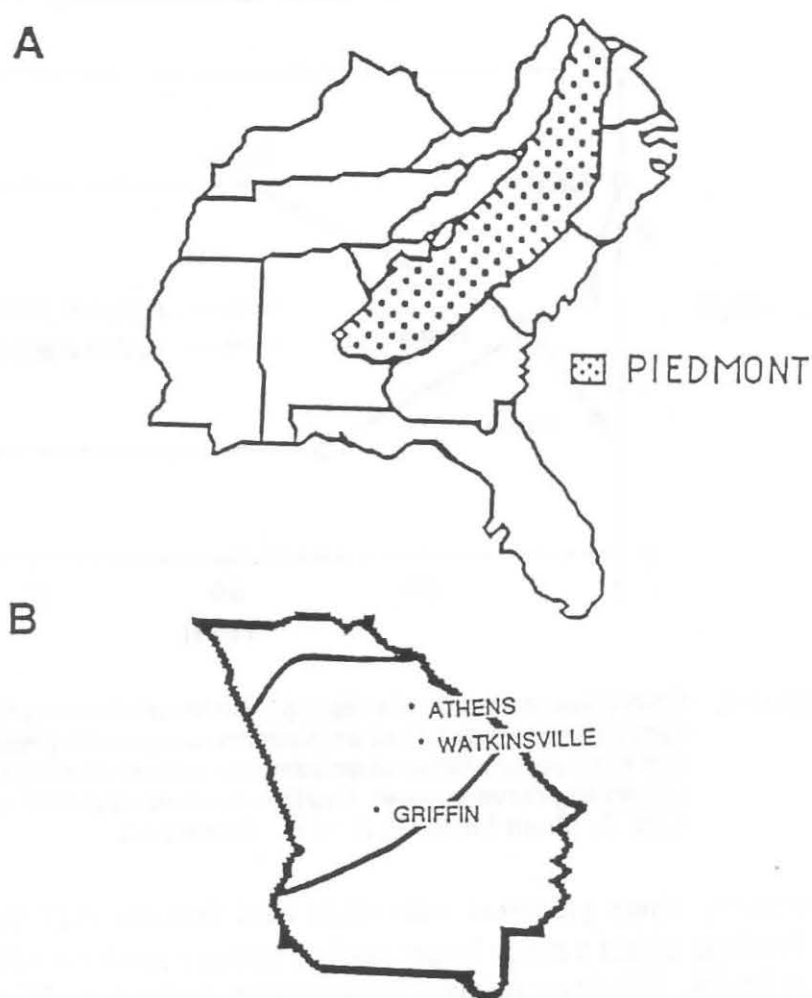


Figure 3. The Southern Piedmont region of the U.S. (A) and locations of proposed research sites on the Georgia Piedmont (B). (From Hendrix, P. F. et al., Unpublished.)

these depositional processes may limit water movement from earthworm burrows into the bulk soil, having possible impacts on solute movement and retention in the upper soil horizons.

C. Standing Stocks, P/B Ratios, and Overall Energetic Status of the Soil Biota in Managed and Natural Ecosystems

It has been a matter of general knowledge among microbial ecologists that bacteria and fungi are strongly limited by available energy sources, and are in a state of starvation much of the time (Clark, 1968; Paul and Clark, 1989). Clarholm (1985) noted a marked contrast between theoretical minimum generation times (hours) vs the average actual time intervals (several to many months) per generation of bacterial or fungal biomass production. In contrast, a much smaller biomass of microbivorous protozoa (chiefly flagellates and amoebas) will prey upon primary decomposers, and have as much as ten doublings or turnovers per season. This follows from more general concepts in the ecological

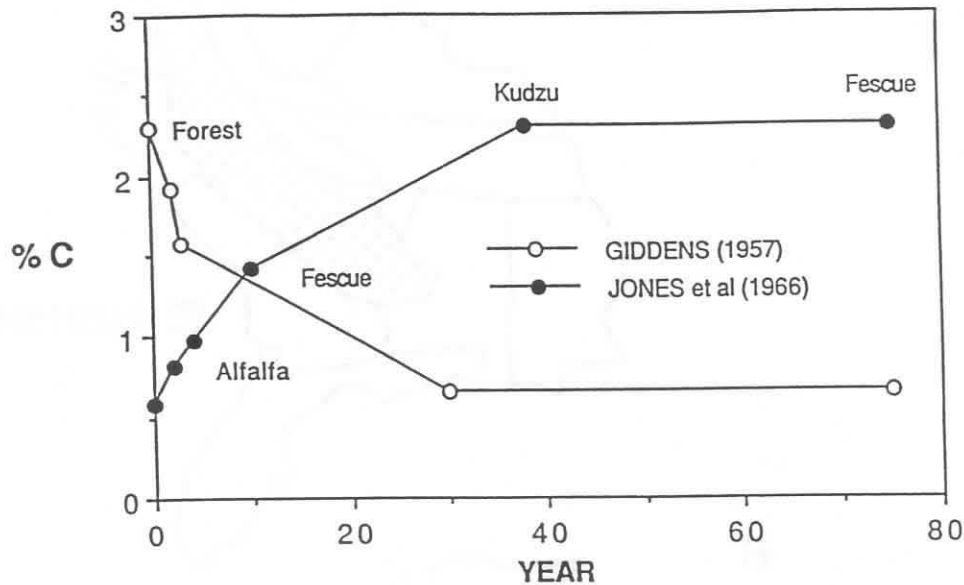


Figure 4. Chronosequences on the Georgia Piedmont show rapid losses of soil organic carbon when undisturbed ecosystems are plowed (descending curve ○—○, and rapid accumulation when intensive cultivation of agroecosystems is ceased (ascending curve ●—●). Equilibrium levels appear to range between 0.6 and 2.3% C. (From Bruce, R. R. et al., Submitted.)

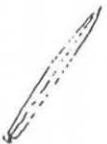
literature, where predators with small total biomass may (by being very active in feeding) affect a much larger pool of primary producers (e.g., phytoplankton, [Brylinsky, 1980]) or primary decomposers (microbes, [Coleman et al., 1983; Laybourn-Parry, 1984]).

In fact, if one examines a much wider spectrum of the soil biota (i.e., the entire heterotrophic assemblage of mesofauna and macrofauna), some remarkably similar patterns emerge as well. As part of a general synthesis of soil biotic activities in both agroecosystems and grasslands (Hendrix et al., 1987; Hunt et al., 1987, and Parmelee et al., 1990) we made a series of comparisons of microbivorous nematodes, collembola, mites, enchytraeids, and earthworms (Table 4). In every case, whether in water films (nematodes and protozoa) or open soil pores (all other faunal groups) there were marked differences between theoretical vs actual secondary production and turnover rates. Minimum generation times in soil are low (usually a few hundred hours, given unlimited food); and actual generation times, expressed as “estimated turnover times per season” are only two to three or less per year. The only exception is a few groups of protozoans, principally the amoebas and flagellates.

Certain groups, e.g., mites and collembola, have a wide range of feeding specificities, which have been extensively reviewed (Moore et al., 1988). However, since we are looking for broad general patterns of population behavior, we do not consider it necessary to break the food chains down further in this more general system-level presentation.

As noted earlier in the organic matter quality section, one of the major differences between our studies and those from cooler climates (e.g., Clarholm,

Table 4. Average Standing Crop and Energetic Parameters for Microorganisms, Mesofauna, and Earthworms in a Lucerne Ley and Georgia No Tillage Agroecosystem

	Naked amoebas	Flagellates	Ciliates	Bacteria	Fungi	Microblvorous nematodes	Collembola	Mites	Enchytraeids	Earthworms
										
Typical size in soil	30 μm	10 μm	80 μm	0.5–1 $\times$ 1–2 μm	$\varnothing$ 2.5 μm 1.0–5.5 μm	$\varnothing \sim 40 \mu\text{m}$	$\varnothing$ 5000 μm	$\varnothing$ 1000 μm	$\varnothing$ 1000 μm	$\varnothing$ 5000 μm
Mode of living	In water films on surfaces	Free-swimming in water films		On surfaces	Free and on surfaces	In water films free and on surfaces	Free	Free	Free	Free in soil
Biomass (kg DW/ha)	95%	5%	<1%	500–750 ^b	700–2700 ^c	1.5–4 ^d	0.2–0.5 ^d	2–8 ^d	1–8 ^d	25–50 ^d
% active	0–100	50 ^a		15–30	2–10	0–100	80–100	80–100	?	0–100
Estimated turnover times/season		10		2–3	0.75	2–4	2–3	2–3	?	3
No. of bacteria/division $\times 10^{-3}$	3–8	0.6–1	20–2000							
Minimum generation time in soil (hr)		2–4		0.5	4–8	120	720	720	170	720

Source: Modified from Clarholm, 1985; Hendrix et al., 1987; and Beare et al., submitted.

Note: DW, dry weight; $\varnothing$, diameter.

^a MPN technique.

^b Direct counts plus size-class estimations.

^c Direct estimation of total hyphal length and diameter.

^d Extractions and sorting.

1985; Elliott and Coleman, 1988) is in microbial production and turnover. Our estimates are about two times greater than theirs, which may be indicative of a more vulnerable labile organic matter pool, perhaps reflecting differences in mean annual temperatures.

Energetically, these patterns should be expected, but the generality of the occurrence has not been noted before. Mesofauna and several components of the macrofauna can enter quiescent, anabiotic states and become reactivated a few minutes or hours after the stimulus of a wetting front or new food or substrate coming within reach (e.g., the passage of a new root or other labile carbon-rich substrate within its sphere of activity). Therefore, losses of the fauna to mortality may be more often due to predation rather than a result of abiotic impacts on these groups of organisms.

IV. DISCUSSION AND CONCLUSIONS

Using several examples, we have attempted to give an overview of biological processes in agroecosystems and their occurrence against a backdrop of a multi-phasic physical milieu. The soil microenvironments, thousands of independent ones per cubic centimeter, are in turn influenced on several micro- and mesoscales by microbial, faunal, and plant interactions.

Human interventions in agroecosystems, particularly in lower impact agricultural systems which employ conservation residue management techniques, such as no tillage, have a profound impact on extent and timing of nutrient cycling in these systems. The opportunities for new research in both temperate and tropical agroecosystems are great, as shown by the series of papers appearing in the reference section of this chapter.

REFERENCES

- Beare, M. H., Neely, C. L., Coleman, D. C., and Hargrove, W. L. 1990. A substrate-induced respiration (SIR) method for measurement of fungal and bacterial biomass on plant residues. *Soil Biol. Biochem.* 22:585–594.
- Beare, M. H., Parmelee, R. W., Hendrix, P. F., Cheng, W., Coleman, D. C., and Crossley, D. A., Jr. 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecol. Monogr.* 62:569–591.
- Bruce, R. R., Langdale, G. W., and Hendrix, P. F. In press. Soil climate dimensions for crop culture technology transfer. ASA Special Publication, Madison, WI.
- Brylinsky, M. 1980. Estimating the productivity of lakes and reservoirs, in: E. D. LeCren and R. H. Lowe-McConnell (Eds.), *The Functioning of Freshwater Ecosystems*. Cambridge University Press, U.K., pp. 411–418.
- Clarholm, M. 1985. Possible roles for roots, bacteria, protozoa and fungi in supplying nitrogen to plants, in A. H. Fitter, D. Atkinson, D. J. Read, and M. B. Usher (Eds.), *Ecological Interactions in Soil*. Blackwell Sci. Pub., Oxford, pp. 355–365.

- Clark, F. E. 1968. The growth of bacteria in soil, in T. R. G. Gray and D. Parkinson (Eds.), *The Ecology of Soil Bacteria*. University of Toronto Press, Toronto, pp. 441–457.
- Coleman, D. C. and Hendrix, P. F. 1988. Agroecosystems processes, in: L. R. Pomeroy and J. Alberts (Eds.), *Concepts of Ecosystem Ecology, A Comparative View*. Springer-Verlag, New York, pp. 149–170.
- Coleman, D. C., Reid, C. P. P., and Cole, C. V. 1983. Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* 13:1–55.
- Crossley, D. A., Jr., Mueller, B., and Perdue, J. C. 1992. Biodiversity of microarthropods in agricultural soils: relations to processes. *Agric. Ecosystem Environ.* 40:37–46.
- Doran, J. W. 1980. Soil microbial and biochemical changes associated with reduced tillage. *Soil Sci. Soc. Am. J.* 44:765–771.
- Elliott, E. T. and Cole, C. V. 1989. A perspective on agroecosystem science. *Ecology* 70:1597–1602.
- Elliott, E. T. and Coleman, D. C. 1988. Let the soil work for us. *Ecol. Bull. (Copenhagen)* 39:23–32.
- Hendrix, P. F., Parmelee, R. V., Crossley, D. A., Jr., Coleman, D. C., Odum, E. P. and Groffman, P. 1986. Detritus food webs in conventional and no-till agroecosystems. *Bioscience* 36:374–380.
- Hendrix, P. F., Crossley, D. A., Jr., Coleman, D. C., Parmelee, R. W., and Beare, M. H. 1987. Carbon dynamics in soil microbes and fauna in conventional and no-tillage agroecosystems. *INTECOL Bull.* 15:59–63.
- Hendrix, P. F., Crossley, D. A., Jr., Blair, J. M., and Coleman, D. C. 1990. Soil biota as components of sustainable agroecosystems, in C. A. Edwards, R. Lal, P. Madden, R. H. Miller, and G. House (Eds.), *Sustainable Agricultural Systems*. Soil and Water Conservation Society, Ankeny, IA, pp. 637–654.
- Holland, E. A. and Coleman, D. C. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. *Ecology* 68:425–433.
- Hunt, H. W., Coleman, D. C., Ingham, E. R., Ingham, R. E., Elliott, E. T., Moore, J. C., Rose, S. L., Reid, C. P. P., and Morley, C. R. 1987. The detrital food web in a shortgrass prairie. *Biol. Fertil. Soils* 3:57–68.
- Laybourn-Parry, J. 1984. *A Functional Biology of the Free-Living Protozoa*. University of California Press, Berkeley.
- Moore, J. C., Walter, D. E., and Hunt, H. W. 1988. Arthropod regulation of micro- and mesobiota in belowground detrital food webs. *Annu. Rev. Entomol.* 33:419–439.
- Mueller, B., Beare, M. H., and Crossley, D. A., Jr. 1990. Soil mites in detrital foodwebs of conventional and no-tillage agroecosystems. *Pedobiologia* 34:389–401.
- Neely, C. L., Beare, M. H., Hargrove, W. L., and Coleman, D. C. 1991. Relationship between fungal and bacterial substrate-induced respiration, biomass and plant residue decomposition. *Soil Biol. Biochem.* 23:947–954.
- Paul, E. A. and Clark, F. E. 1989 *Soil Microbiology and Biochemistry*. Academic Press, San Diego, CA.
- Parmelee, R. W., Beare, M. H., Cheng, W., Hendrix, P. F., Rider, S. J., Crossley, D. A., Jr., and Coleman, D. C. 1990. Earthworms and enchytraeids in conventional and no-tillage agroecosystems: a biocide approach to assess their role in organic matter breakdown. *Biol. Fertil. Soils* 10:1–10.

- Pesek, J., Brown, S., Clancy, K. L., Coleman, D. C., Fluck, R. C., Goodman, R. M., Harwood, R., Heffernan, W. D., Helmers, G. A., Hildebrand, P. E., Lockeretz, W., Miller, R. H., Pimentel, D., Qualset, C. O., Raun, N. S., Reynolds, H. T., and Schroth, M. N. 1989. *Alternative Agriculture*. Committee on the Role of Alternative Farming Methods in Modern Production Agriculture. Board on Agriculture, National Research Council. National Academy Press, Washington, DC, pp. 448.
- Sanchez, P. A., Palm, C. A., Szott, L. T., Cuevas, E., and Lal, R., with Fownes, J. H., Hendrix, P. F., Ikawa, H., Jones, S., van Noordwijk, M., and Uehara, G. 1989. Organic input management in tropical agroecosystems, in D. C. Coleman, J. M. Oades, and G. Uehara (Eds.), *Dynamics of Soil Organic Matter in Tropical Ecosystems*. NIFTAL Project, University of Hawaii Press, Honolulu, pp. 125–152.
- West, L. T., Hendrix, P. F., and Bruce, R. R. 1991. Micromorphic observation of soil alteration by earthworms. *Agriculture, Ecosystems and Environment* 34:363–370.